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Sons do not take advantage of a head start: parity in herring gull offspring sex ratios despite greater initial investment in males

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Skewed adult sex ratios sometimes occur in populations of free-living animals yet the proximate mechanisms, timing of sex-biases, and the selective agents contributing to skew remain a source of debate with contradictory evidence from different systems. We investigated potential mechanisms contributing to sex biases in a population of herring gulls with an apparent female skew in the adult population. Theory predicts that skewed adult sex ratios will adaptively lead to skewed offspring sex ratios to restore balance in the effective breeding population. Parents may also adaptively bias offspring sex ratios to increase their own fitness in response to environmental factors. Therefore, we expected to detect skewed sex ratios either at hatching or at fledging as parents invest differentially in offspring of different sexes. We sampled complete clutches (n = 336 chicks) at hatching to quantify potential skews in sex ratios by position in the hatch order, time of season, year, and nesting context (nest density), finding no departure from equal sex ratios at hatching related to any of these factors. Further, we sampled 258 chicks at near-fledging to investigate potential sex biases in survival at the chick stage. Again, no biases in sex ratios were recorded. Male offspring were favored in this population via greater maternal investment in eggs carrying male embryos and greater parental provisioning of male offspring which reached greater sizes by fledging. Despite the advantages realized by male offspring, females were equally as likely to fledge as males. Thus, biased adult sex ratios apparently arise in the post-fledging and pre-recruitment stage in our population.

Skewed adult sex ratios should be maladaptive in species with obligate bi-parental care because capable individuals will undoubtedly be excluded from the effective breeding population when a surplus of one sex exists. Biases in the sex ratio favoring females, however, have been widely reported in seabirds leading to males breeding at an earlier age than females (Hunt et al. 1980) and female–female social pairs (Ryder 1983, Nisbet and Hatch 1999, Lorenstsen et al. 2000, Nisbet et al. 2007, Bried et al. 2009). Although female–female pairings often successfully fledge offspring that are sired via extra-pair copulations, these pairings may not be as successful, on average, as male–female pairings (Young et al. 2008, Young and VanderWerf 2013).

Fisher (1958) proposed that equal investment in offspring of both sexes is an evolutionarily stable strategy and that frequency-dependent selection pressure should lead to the overproduction of the sex that was underrepresented in the adult population. In theory, fitness should increase for parents producing the underrepresented sex because more of their offspring will be recruited into the breeding population. Sex ratios may also be biased if the relative costs of producing male and female offspring differ, ultimately influencing parental fitness (Frank 1990). If the relative fitness (or cost) of male and female offspring differs with environmental conditions, then adaptive sex ratio theory predicts that a female will produce more of the sex that maximizes her own fitness (Trivers and Willard 1973). From the perspective of chick survival, the sex that demands the greatest energetic investment (the larger sex in dimorphic species) will suffer greater mortality when resources are limited (barring any sex-related dominance relationships among siblings), so females will bias clutches in favor of the least expensive sex when conditions are poor.

Sex ratios could be manipulated by the parents via numerous pathways, yet the mechanisms leading to sex biases remain poorly understood. The heterogametic sex (females, in birds) could manipulate the primary sex ratio of her eggs in response to environmental and social cues (Clutton-Brock et al. 1985, Alonso-Alvarez 2006). In species with asynchronous hatching, altering the order in which eggs of different sexes are laid would effectively lead to sex biases at fledging because the early-to-hatch chicks are at a considerable advantage over their younger siblings (Bollinger 1994, Nisbet and Szczys 2001, Savoca et al. 2011, Benito et al. 2013). Sex ratios at fledging could also be biased by females depositing more resources in the eggs of a particular sex so that the embryo hatches with a size advantage and a head start in sibling–sibling competition for resources. Egg size appears to carry-over to influence nestling development as chicks hatching from larger eggs tend to grow at faster rates (Schifferli 1973). Even if at hatching both sexes are equally common, parents could preferentially feed chicks of one sex and bias growth rates and survival at the chick stage or post-fledging (Schauroth and Becker 2007).

Many species of birds demonstrate parity in sex ratios at hatching, but differential mortality between hatching and fledging can lead to biased sex ratios (reviewed by Clutton-Brock 1986). Seasonal changes in offspring sex ratios could also lead to biased adult ratios because chicks hatched earlier in the nesting season are often more likely to recruit into the breeding population (Hochachka 1990, Cordero et al. 2001). In colony-nesting species, offspring sex biases may even be correlated with spatial patterns within the colony where territory quality is heterogeneous (Suorsa et al. 2003, Bell et al. 2013, Minias et al. 2014).

The numerous pathways potentially leading to skewed adult sex ratios remain an issue of research interest because previous studies yield mixed results. Further, many studies only report ratios of sexes when the offspring approach independence, thereby missing information on sex ratios at hatching. Few studies examine sex ratios at hatching and then follow the fate of those offspring through the chick development period until fledging (but see Szczys et al. 2001).

Here, our objectives are to quantify offspring sex ratios at hatching and fledging in a declining population of herring gulls *Larus argentatus* (Ellis et al. 2007) with an apparent female-biased adult population (Burger and Gochfeld 1981) in order to identify the factors contributing to the skewed adult sex ratio. Following Fisher's evolutionary stable sex allocation theory, we expect a male-biased offspring sex ratio in our population. If, however, sex ratios vary according to the adaptive sex allocation theory, then we may expect spatial or temporal variability in sex ratios. Herring gulls show a high degree of sexual size dimorphism with adult males being approximately 12% heavier than females in our population (male mean mass = 1147 g, female mean mass = 1023 g, Pierotti and Good 1994), suggesting that raising male offspring is more costly than raising female offspring. If resources are limited, therefore, adults should produce more female offspring (the less-expensive sex, Myers 1978). In addition, previous research in our study system has detected strong spatial influences on reproductive success based on nest density (Savoca et al. 2011), so here we also examine how local nest density may be related to offspring sex ratios, predicting a male-biased ratio in the most dense (generally highest-quality) nesting territories.

Methods

Herring gull reproduction was studied on Appledore Island, Maine, USA, a 38 ha island located in the Gulf of Maine (42°59′21″N, 70°36′52″W) with approximately 750 nesting pairs. Nests were randomly selected for monitoring during the incubation stage in three seasons (2011 [n = 55 nests], 2012 [n = 33], and 2013 [n = 24]). Nests and eggs were labeled, egg measurements recorded (maximum length and width), and nests monitored daily. Multiple checks were conducted daily as eggs hatched and hatching chicks were marked with coloured marker on their egg tooth while still in the egg in order to link chicks to egg of origin and identify hatch order among first (hereafter 'A chick'), second (B) and third (C) chicks. Upon hatching, each chick was painted with colour-coded markers (days 1–9) or coloured leg rings (after day 9) for subsequent identification. A small blood sample was extracted on hatch day for genetic analyses of sex ratios (see below). To quantify growth rates, individually identifiable chicks were weighed and head + bill measurements (back of the skull to the tip of the bill) recorded on days 1, 3, 5, 7, and 9 after hatching. Chick survival was monitored by daily searches of nesting territories for the presence or absence of each uniquely marked chick.

Chicks that survived to near-fledging were captured for banding during mid-July in each season. This sample included a subset of birds monitored daily as well as chicks from unmonitored nests. Blood samples were also extracted from these near-fledging age chicks for genetic sexing.

DNA extractions and PCR amplifications were conducted in a laboratory where pre- and post-PCRs are spatially separated, and assembled using dedicated pre-PCR equipment and aerosol-resistant barrier pipette tips. DNA was extracted from the blood samples using a DNeasy Blood and Tissue kit for whole DNA extraction (QIAGEN, Valencia, CA, USA) or E-Z 96 Blood DNA Kit (Omega Bio-Tek, Norcross, GA) into individual U-prep tubes (Harvey et al. 2006). PCR reactions amplified diagnostic sex-linked alleles using the 2250F, 2718R primer set (Griffiths et al. 1998) that has previously been used successfully to sex herring gulls and other avian taxa (Harvey et al. 2006). Amplification volumes totaled 10 ul and included genomic DNA, 10 mM Tris-HCl reaction buffer, equal portions of primers at 10 mM concentrations and 10 mM dNTPs (Invitrogen, Carlsbad, CA, USA). We visualized 10 ul of each PCR sample on a 2% agarose gel containing 0.025 mg ethidium bromide per ml. Gels were run in tris-acetate-EDTA buffer (Sambrook and Russell 2001) at a voltage of 120 V for approximately 35 min. A 5 ug aliquot of a 1-Kb Plus™ DNA ladder (Invitrogen, Carlsbad, CA, USA) was run with each row of samples as an unambiguous size standard. We photographed gels under UV light using a Gel Logic 100 Imaging System and assigned sex by counting the number of visible bands in each lane. Because females are the heterogametic sex, two visible bands in a lane indicated that the sample was from a female. Of 336 hatching day blood samples, the sex of 335 chicks was identified and the remaining chick was excluded from analyses.

Statistical methods

Initial tests for sex ratio biases at hatching and near-fledging were implemented using goodness of fit χ^2 tests where a significant difference would indicate a departure from the 0.5 male/0.5 female expectation (SAS Inst. 2003, ver. 9.3). Only complete 3-egg clutches with known hatch orders were included in the analysis (n = 112 nests). Nests lacking 3 eggs were excluded because most nests with fewer than 3 eggs are likely the result of incomplete nest predation and true hatching order could not be determined for the remaining eggs.

At the clutch level, we further tested the possibility that overproduction of male offspring by some females was balanced by overproduction of female offspring by other females such that the Mendelian expectation of a 1:3:3:1 (MMM:MMF:MFF:FFF) clutch sex ratio was violated. We tested for this possibility using a goodness of fit χ^2 test for 111 complete clutches (Postma et al. 2011).

We tested the multiple pathways that could lead to a biased sex ratio at hatching using a generalized linear mixed model (PROC GLIMMIX) with binomial error distribution where the sex of the offspring (dependent variable) was modeled as a function of position in the hatching order, egg volume, hatch date (day after 26 May, the first date that an egg hatched in any season), year, and the average distance from the chick's nest to the three nearest neighboring nests as a measure of nest site density. Egg volume was calculated as egg length × width^2 × 0.476 (Harris 1964). Because the same female presumably laid all three eggs within each nest, the nest identifier was included as a random variable.

To test for potential differences in growth rates between the sexes or by position in the hatching order, we constructed a mixed model testing for differences in weight and head + bill length (two separate dependent variables) as related to age, the age × sex interaction, and the age × hatching order interaction with nest identification as a random variable because multiple chicks were sampled from each nest (PROC Mixed). Least squares means and standard errors calculated from the mixed models are reported.

We conducted mark–recapture survival analyses in Program MARK (White 2013, ver. 6.1) to test for differences in survival between male and female chicks monitored daily in 2012 and 2013. The presence (1) or absence (0) of chicks were recorded for 7 weeks following the hatch day for each individual bird creating an encounter history file with 7 encounter occasions. We held recapture probabilities constant in all models because living chicks are rarely missed during a week of daily observations. Preliminary analyses indicated weekly recapture probabilities (p) > 0.95. The model set for our survival analyses included models where survival probabilities were allowed to vary by sex or age (week) and a null model (no influence of sex or age on survival probabilities, Table 1).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1s2p7> (Bonter et al. 2015).

Results

Across all years and hatch order positions, we detected no deviation from an even sex ratio at hatching ($\chi^2 = 0.07$, DF = 1, n = 335, p = 0.785) with 170 male chicks and 165 female chicks identified in 112 nests. Sex ratios did not differ from parity among A, B or C chicks. In both A and B chicks, 57 individuals were male and 55 female ($\chi^2 = 0.04$, DF = 1, n = 112, p = 0.850). C chicks also demonstrated parity with 56 males and 55 females ($\chi^2 = 0.01$, DF = 1, n = 111, p = 0.924). Sexes of gull chicks that survived to near fledging were at parity ($\chi^2 = 0.992$, DF = 1, n = 258, p = 0.319, Fig. 1). At the clutch level, sex ratios of complete clutches did not violate the 1:3:3:1 Mendelian expectation ($\chi^2 = 2.03$, DF = 3, p = 0.566, MMM = 18, MMF = 38, MFF = 39, FFF = 16).

Table 1. Mark–recapture models testing the influence of chick sex and age (week) on survival probabilities (ϕ). Resighting probability (p) was held constant in all models. The model representing variable survival by age was best supported by the data.

Model	AICc	Delta AIC	Model weight	Parameters
$\phi_{(age)}\, p_{(\cdot)}$	666.3	0	0.89	7
$\phi_{(.)}\, p_{(\cdot)}$	671.3	5.02	0.07	2
$\phi_{(sex)}\, p_{(\cdot)}$	673.3	6.97	0.03	3
$\phi_{(sex*age)}\, p_{(\cdot)}$	675.2	8.89	0.01	13

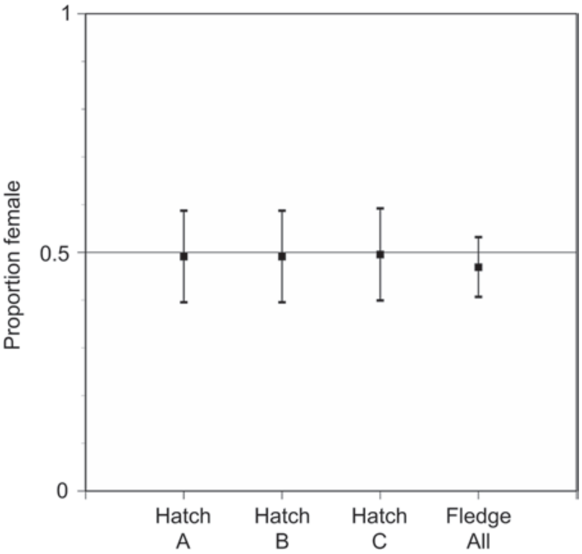

Figure 1. The sex of herring gull chicks did not vary from parity at hatching for any position in the hatching order (A, B or C chicks, n = 112 complete clutches). A separate sample of chicks approaching fledging-age (n = 258) was also at parity. Mean proportion female and 95% confidence limits from the χ^2 goodness of fit tests are reported.

Sex of offspring at hatching did vary with egg volume as females were more likely to hatch from smaller eggs than males (GLIMMIX model, $F_{1,125} = 4.90$, p = 0.029, Fig. 2a). As suggested by the χ^2 tests, sex ratios were unrelated to position in the hatch order within clutches ($F_{2,125} = 2.47$, p = 0.089). We found no evidence of sex ratios differing among years ($F_{2,125} = 0.38$, p = 0.685) nor through the nesting season (hatch date, $F_{1,125} = 1.62$, p = 0.205, Fig. 2b), nor did we find any relationship between nesting density and sex ratios ($F_{1,125} = 1.43$, p = 0.234, Fig. 2c).

Chick weights increased with age (mixed model, age effect, $F_{1,1146} = 4801.68$, $p < 0.001$, Fig. 3a). Tests for differential growth rates revealed that males gained weight faster than females (age × sex interaction, $F_{2,1146} = 6.60$, p = 0.010, Fig. 3a), and, controlling for sex, the first and second chicks to hatch reached greater mass by day 9 ($A_{Mean} = 202.4$ g ± 4.8 g, $B_{Mean} = 200.7$ g ± 4.8 g) than C chicks ($C_{Mean} = 166.7$ g ± 4.8 g, age × hatch order interaction, $F_{2,1146} = 122.28$, $p < 0.001$). Analyses of the head + bill measurements also demonstrated that chicks grew with age (age effect, $F_{1,1147} = 8645.73$, $p < 0.001$), that males grew faster than females (age × sex interaction, $F_{1,1147} = 34.40$, $p < 0.001$, Fig. 3b), and the first and second chicks to hatch in a clutch were larger on day 9 ($A_{Mean} = 65.9$ mm ± 0.5 mm, $B_{Mean} = 65.7$ mm ± 0.5 mm) than the C chicks ($C_{Mean} = 62.9$ mm ± 0.5 mm, age × hatch order interaction, $F_{2,1147} = 134.18$, $p < 0.001$).

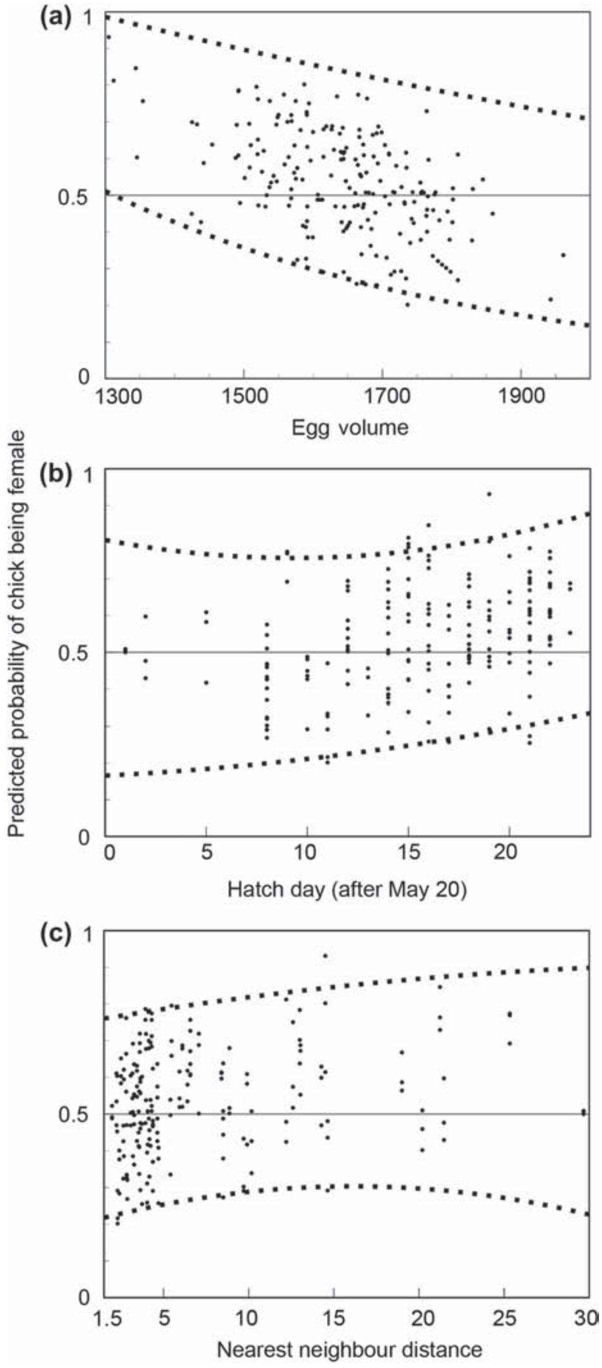

Figure 2. The sex ratio of herring gulls chicks at hatching varied by egg volume with female offspring more likely to hatch from smaller eggs (a), but sex ratios were unrelated to hatching date (b) or the mean distance in meters to the three nearest neighboring nests (c). Predicted values from the GLIMMIX model are presented with 95% confidence limits.

Mark–recapture analyses of 161 chicks followed in 2012 and 2013 provided no support for sex-based differences in weekly survival probabilities regardless of a chicks' position in the hatching order (Fig. 4a, Table 1). Weekly survival probabilities averaged 0.84, leading to an overall 7-week survival probability of < 0.3. Survival probabilities did vary with age (Table 1) as mortality rates were greatest, on average, in the first two weeks post-hatching (Fig. 4b).

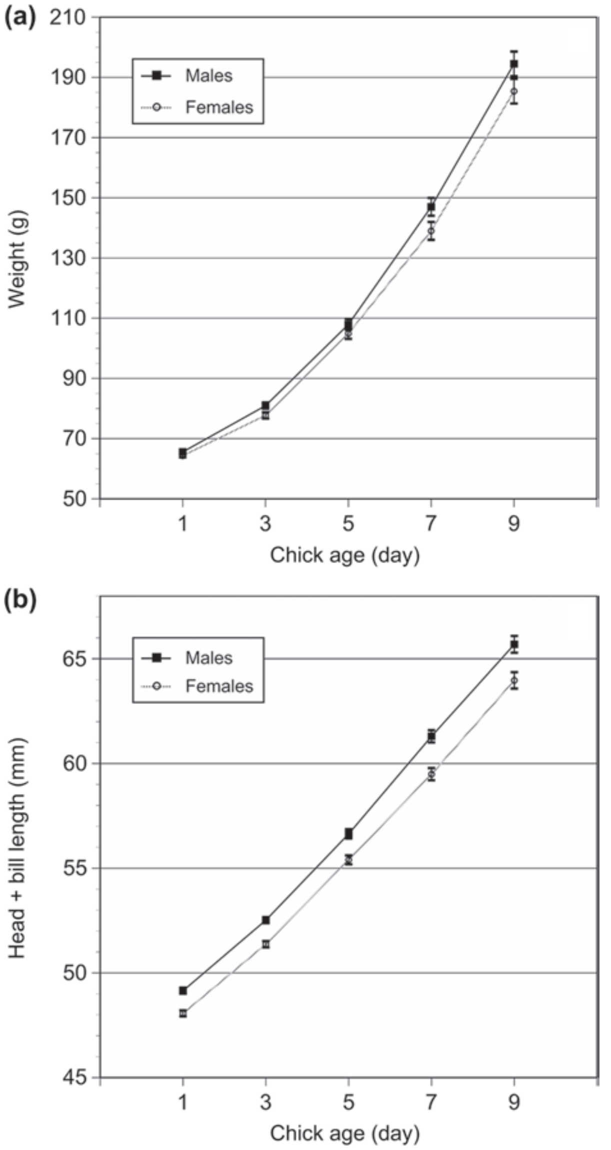

Figure 3. Male herring gull chicks were heavier (a) and grew faster (b), on average than female chicks regardless of position in the hatch order. Least squares means and standard errors calculated from the mixed models are reported.

Discussion

Sex ratios of herring gull chicks at hatching and fledging were at parity despite greater parental investment in males. Male offspring were favored in this population via greater female investment in eggs carrying male embryos and greater parental provisioning of male offspring to maintain sexual size dimorphism. An alternative interpretation is that male herring gull chicks require a biased parental investment in order to fledge in equal numbers as females in this population. Regardless of the framing, parity of offspring sex ratios at fledging fails to rectify the apparent skew in adult sex ratios suggesting that males do not take advantage of greater parental investment.

Although numerous studies have quantified sex ratios at laying or hatching in order to test for biased sex ratios, conflicting results demonstrate a continuing gap in our

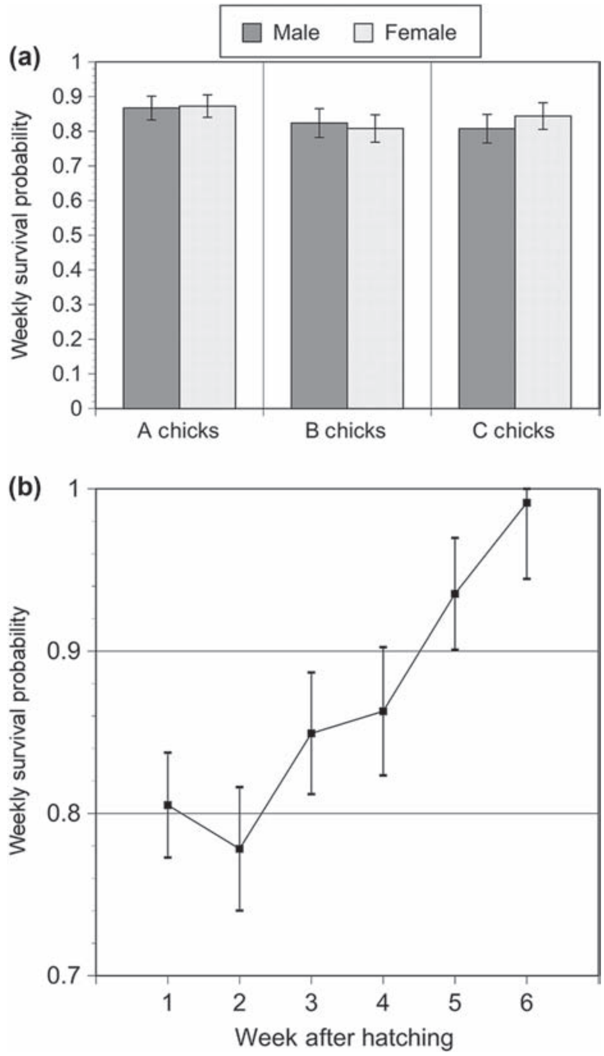

Figure 4. Weekly survival probabilities from chicks monitored in 2012 and 2013 (n = 161) did not vary based on sex of the chicks (a) according to estimates and standard errors from the model [$\phi_{(sex)}\ p_{(.)}$] in Program MARK. Weekly survival probabilities increased with age (b) as estimated by the model [$\phi_{(age)}\ p_{(.)}$].

knowledge. Many studies of birds failed to detect biased sex ratios (Heinsohn et al. 1997, Nager et al. 2000, Genovart et al. 2003, Husby et al. 2006, Zielińska et al. 2010) while other studies found a female bias (Szczys et al. 2001, Neto et al. 2010) and yet others reported a male bias (Bednarz and Hayden 1991). Studies have even recorded variation in offspring sex ratios within the same species sampled at different locations (Rosivall et al. 2004) or at the same location in different years (Rubolini et al. 2009).

We found no evidence of skew in sex ratios by position in the hatching order, a mechanism that could dramatically favor one sex over another. This parity throughout the clutch is important because egg size tends to decrease throughout the laying order favoring the chicks hatching from earlier eggs (Chin et al. 2012, Bowers et al. 2013). Further, seniority within the nest is directly related to offspring growth and survival due to sibling competition (Bonisoli-Alquati et al. 2011). In systems where larger males achieve greater reproductive success, male-biased sex ratios are predicted among first chicks within a clutch because the expected effect on offspring fitness of being raised under advantageous circumstances is greater for males than for females (Trivers and Willard 1973). Alternatively, the smaller sex may be favored early in the clutch because early hatching would help offset the significant size disadvantage in contests with the larger sex in sibling–sibling competition. No clear pattern exists, however, with regard to sex and hatching order across taxa or even within the closely-related *Larus* gulls. As in our study, laying order did not predict sex of the embryo in yellow-legged gulls *Larus michahellis* (Rubolini et al. 2009) or lesser black-backed gulls *L. fuscus* (Griffiths 1992). But the first chick to hatch in a clutch was more likely to be male whereas the last chicks to hatch in a clutch was more likely to be female in black-headed gulls *Chroicocephalus ridibundus* (Lezalova et al. 2005) and ring-billed gulls *Larus delawarensis* (Meathrel and Ryder 1987). We did find that growth rates were related to position in the hatch order, with first and second chicks growing at a faster rate than third chicks, and males maintained a size advantage over females beginning almost immediately after hatching, similar to previous research with herring gulls (Kim and Monaghan 2006).

Studies testing for relationships between egg size and offspring sex have also achieved mixed results. Sexual egg size dimorphism could be adaptive and variable depending on mating system or the strength of competitive relationships among siblings. As in the current analysis, the volume of male eggs was greater than female eggs in a study of white-crowned sparrows *Zonotrichia leucophrys* (Mead et al. 1987). The opposite pattern was found in spotless starlings *Sturnus unicolor* where eggs containing female embryos were significantly heavier than eggs containing male embryos (Cordero et al. 2001). No differences, however, were detected in the size of eggs holding male and female embryos in parrot finches *Erythrura trichroa* (Pryke and Rollins 2012), house wrens *Troglodytes aedon* (Bowers et al. 2013), ring-billed gulls (Meathrel and Ryder 1987), lesser black-backed gulls (Griffiths 1992), roseate terns *Sterna dougallii* (Szczys et al. 2001), or common terns *S. hirundo* (González-Solís et al. 2005). In one study of black-headed gulls, egg volume was unrelated to offspring sex (Lezalova et al. 2005) whereas another study in the same species found that males hatched from heavier eggs than females within clutches (Müller et al. 2005a). No sexual egg size dimorphism was detected in the overall size of ring-billed gull eggs, but egg constituents varied by sex of the embryo wherein eggs with female embryos contained more yolk than eggs with male embryos (Chin et al. 2012), suggesting greater maternal investment in female offspring. Although no clear pattern exists with regard to biased maternal investment in eggs based on offspring sex, egg size may have lasting effects through greater survival of offspring that hatched from larger eggs (Bolton 1991).

If the sex ratio at hatching is at parity, differential survival during the chick stage could lead to sex biases in the adult population. Differential mortality among sexes between hatching and fledging appears to increase as food resources decline, and theory predicts that the more expensive sex (requiring more resources) will suffer disproportionate mortality. We failed to find sex biases in mortality during the chick stage, a result similar to studies of common terns

(Benito et al. 2013) and roseate terns (Nisbet and Szczys 2001). Evidence of greater rates of male pre-fledging mortality, however, was found in western gulls *Larus occidentalis* (Sayce and Hunt Jr 1987), black brant *Branta bernicla nigricans* (Lemons et al. 2012), rooks *Corvus frugilegus* (Roskaft and Slagsvold 1985), lesser black-backed gulls (Griffiths 1992), and in all-male clutches of black-headed gulls (Müller et al. 2005b).

The current study would benefit from information on resource availability and the energetic condition of the nesting pairs. The lack of skew in sex ratios in each of the three years of our study suggests that resource availability, in general, is not influencing sex ratios in our population because resource availability likely varied considerably from year to year. Previous research, however, has produced intriguing results linking resource availability or parental condition to offspring sex ratios or chick survival. In an experiment with yellow-legged gulls, food supplemented females produced larger C-eggs only if the C-egg contained female offspring, indicating that females strategically allocate resources to C-eggs (Saino et al. 2010). Additional feeding experiments found that supplemented females overproduced sons (Kilner 1998, Merkling et al. 2012, Bowers et al. 2013) and that sex ratios varied with clutch size (Arnold et al. 2003). Besides variability in food resources, other environmental drivers including differential exposure to pollutants may also influence offspring sex ratios (Erikstad et al. 2009, 2011, Bouland et al. 2012).

We found no seasonal trends in offspring sex ratios in herring gulls but other studies demonstrate variable results. Time of breeding was not found to influence offspring sex ratios in roseate terns (Szczys et al. 2001), black-headed gulls (Lezalova et al. 2005), western gulls (Sayce and Hunt Jr 1987), or lesser black-backed gulls (Griffiths 1992). A greater female bias in the sex ratio at hatching as the breeding season progressed was documented in Savi's warbler *Locustella luscinioides* (Neto et al. 2010), European kestrels *Falco tinnunculus* (Dijkstra et al. 1990), and great cormorants *Phalacrocorax carbo* (Wojczulanis-Jakubas et al. 2013), whereas the opposite pattern was documented in spotless starlings (Cordero et al. 2001). Further, results are not necessarily consistent within species. The sex ratio of collared flycatchers *Ficedula albicollis* was skewed towards males later in the season in some, but not all, populations (Rosivall et al. 2004). Seasonal variation in sex ratios were detected in yellow-legged gulls with more male offspring early in the breeding season in one season but not in a subsequent year within the same colony (Rubolini et al. 2009). Seasonal changes in sex ratios were demonstrated in the common sandpiper *Actitis hypoleucos* but not in the closely-related spotted sandpiper *A. macularia* (Andersson et al. 2003). And, in great tits *Parus major*, a female bias at hatching was detected in first clutches, but proportions of males and females in second clutches were equal (Lessells et al. 1996).

Spatial patterning of nesting territories in colonially-nesting species are often important and nests in dense aggregations are more successful in our population (Savoca et al. 2011), at least in some years (Bonter et al. 2014). In great cormorants, birds nesting centrally in colonies experienced greater reproductive success than birds on the periphery and produced more male offspring (Minias et al. 2014). Here, however, we failed to find any relationship between offspring sex ratios and the average distance to the three nearest neighboring nests (an indicator of nesting density).

Biases in the adult sex ratio favoring females have been widely reported in birds (Hunt et al. 1980, Sayce and Hunt Jr 1987, Young et al. 2008, Lemons et al. 2012) leading males to attempt breeding at an earlier age (Hunt et al. 1980). Although we lack quantitative data on the sex ratios of our adult population, the widespread pairing of females with young males (birds retaining juvenile plumage) in our population suggests a lack of fully mature males (Burger and Gochfeld 1981). Because our adult population is female biased while sex ratios at hatching are at parity, the question remains – what is happening to young males following fledging that leads to relatively low recruitment into the breeding population?

Differential post-fledging survival among sexes, though difficult to quantify and tease apart from differential dispersal patterns, could lead to biased adult sex ratios (Clutton-Brock et al. 1985). What happens after the chicks fledge from the nesting colony, however, remains poorly understood. Sex-biased mortality may remove males during the post-fledging but pre-recruitment stage, a period that lasts nearly 4 yr in herring gulls. Evidence from other systems supports this hypothesis. A female-biased sex ratio in common terns at fledging was reversed in the post-fledging period as return rates and recruitment into the breeding population were significantly greater for males than for females (Becker et al. 2008), while Sayce and Hunt Jr (1987) concluded that greater post-fledging male mortality in western gulls must be responsible for female biased adult sex ratio.

Variability of results from studies examining sex ratios is cause for caution and no single theory of sex allocation will apply across systems and taxa. Caution is required when interpreting sex-ratio research because many studies lack robust sample sizes or only examine sex ratios at hatching, at fledging, or for a limited number of seasons (Koenig and Dickinson 1996). Our analysis demonstrates that herring gull parents favor male offspring through greater allocation of resources at the egg and chick stages. These advantages, however, do not lead to greater fledging rates for sons – or perhaps are necessary for males to fledge in equivalent numbers as females.

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